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REDUNDANCY IN LIVING ORGANISMS:

FERTILITY VS. BROOD CARE

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Foreword

The occurrence of redundancy in biological systems has been one of the original interests of the Bio-Systems Division. In this report, K. S. Tweedell takes up a very simple instance of redundancy, namely, the production of large numbers of offspring in cases of stable population level. The occurrence of redundancy is correlated with the occurence of another method to insure replacement, namely, brood care. As expected, amounts of redundancy and brood care are negatively correlated. There are wide variations in fecundity even between closely related species; thus, there is no evidence of a critical optimum of redundancy in this instance.

Henry Quastler

Kenyon S. Tweedell

REDUNDANCY IN LIVING ORGANISMS: FERTILITY VS. BROOD CARE

Introduction

It is a matter-of-fact biological phenomenon that in a given environment, populations tend toward constant sizes.[1] The concept of population equilibrium balance or "steady state" advanced by Nicholson (6) and Thompson (10a) provides the background for the present study. In some cases this stability is static in character but often it is of a dynamic nature as evident in numerous examples of fluctuations and oscillations in animal populations.

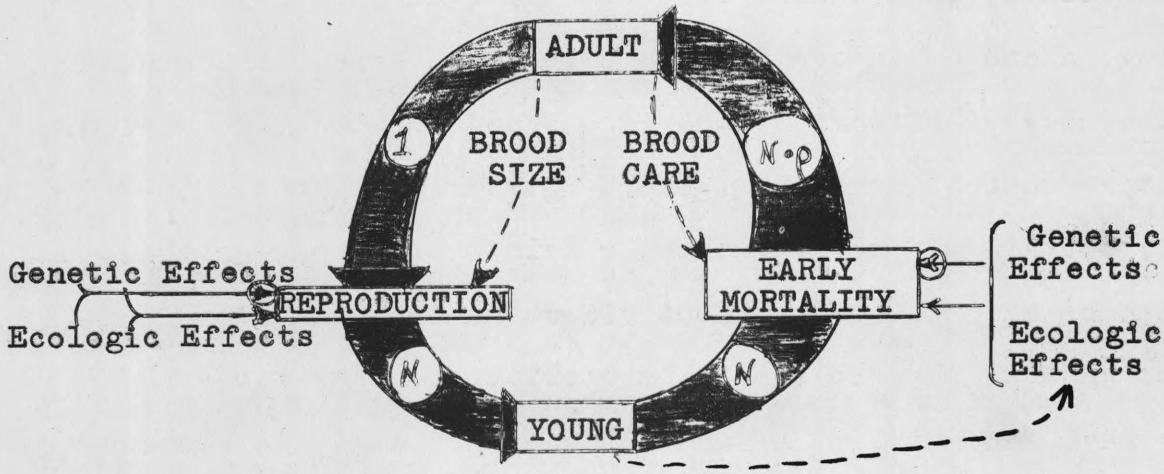
The condition for this stability is a balance between reproduction and mortality. However, equilibrium is not merely the result of these two factors but they in turn are under the influence of genetic, ecological and parental controls (1).

Genetic factors can directly influence the reproduction or mortality of a population as dictated by various genic changes or they can alter the adaptability of that population to a particular environment.

The ecological influence may be exerted by environmental factors, or so-called physico-chemical effects: climate, crowding or by other factors operating through interaction of the species: predation, competition, etc. All of these controls affect the population stability (1).

[1]The growth of both human and animal populations can be divided into a period of exponential growth, a period of equilibrium or stability, and a period of decline.

We are interested, at this time, only in parental control as effected by brood size and brood care. The following grossly simplified scheme shows what is involved:



= Yields
= Increases
= Decreases
= Controls

Ecologic Effects
1. Species Interaction
   Predation
   Niche & Food Competition
   Host-Parasite
2. Environmental
   Climate
   Crowding
   Food Availability
   Disease

Each adult contributes <u>N</u> young (the whole reproductive period is considered as a single event); each of the young is subjected to certain hazards of early life (again, contracted into a single event) which allow only a fraction of the young, <u>p</u>, to escape. The condition for stability is that $N \cdot p = 1$.

To reiterate, both the reproductive period and early mortality are subject to control and adjustment by the environment and by the parents. These controls are interdependent. For example, the chain of effects, "brood size⇒reproduction⇒young⟹

density of predators $\Longrightarrow$ early mortality" forms part of a feedback loop which presumably typifies important factors in the stabilization of population levels. Effective reproduction is guaranteed by producing a sufficiently redundant number of offspring, alone or in combination with brood care. The greater the redundancy of offspring, the less brood care will be needed.

Either control mechanism, brood size or brood care, involves a certain effort. However, elimination of one or the other can be accomplished without affecting the main flow loop. It seems natural that it should be possible to substitute in various ways, one kind of effort for another, e.g., to compensate with increased brood size for lesser brood care, and vice versa. Biological experience suggests that this may indeed be the case.

The pertinent data available are somewhat short of perfect. Ideally, the total number of progeny should be estimated for the entire reproductive life of the parents. However, since data on both the life and reproductive spans is limited, estimations will refer to the litters, clutches, etc., produced in a reproductive season. A frog may lay a few hundred eggs in one clutch and have an egg complement of several thousand for a reproductive season.

Likewise, the effective number of progeny should be estimated as the number reaching sexual maturity. However, the effects of predation and environment are difficult to assess between the time an animal reaches adulthood and reproductive maturity. Therefore, the number of progeny will be considered as those produced at the time of hatching or at the termination of brood care.

I. Survey of stabilizing mechanisms

A. Modes of Fertilization and Earliest Development

Animals can be grouped into 3 categories according to modes of earliest development.

Oviparous animals are those which lay eggs that hatch after they are excluded from the body. Most aquatic animals practice oviparity with external fertilization of the egg masses. However, some of the oviparous group, such as the amphibians, have developed protective fertilization by means of pseudo-copulation. Others, such as the more specialized salamanders, the birds and the reptiles, have adopted internal fertilization.

A modification of oviparity occurs in the ovoviviparous animals, which hatch their eggs within the body of the parent and thus necessitate internal fertilization. This is typical of the snakes and elasmobrach fishes and a few amphibians.

The third category, viviparous animals, produce living young (instead of eggs) from within the body. Again, this requires internal fertilization. Most mammals fall into this category, in which the free larval stages are compressed into the embryonic period; however, this adaptation occurs in several lower organisms as well.

The shift from external to internal fertilization, and from oviparity to viviparity, definitely implies an increased amount of pre-natal brood care. Associated with this change in reproductive habits, there is a trend toward a reduction in the number of ova produced. With scarcity in number, there is a tendency for the eggs to become larger. There are exceptions to this general rule. A great amount of parental care without large egg size or viviparity is also reached when development of the offspring is protected not by the parents, but by the earlier generations of the offspring. Wheeler (11) claims this is the way the social habit developed in the insects.

B. Post-Natal Brood Care

The evolutionary tendency has been toward a lessening of chance survival with a great redundancy of ova toward fewer offspring which receive a great deal more care; still, widely divergent situations are often found within one group of animals. For instance, among the fishes, there are vast differences in egg number; they are associated with the expected differences in amount of brood care. This is readily seen in the following table from Wunder (14).

Marine Fish		Fresh Water Fish	
Without Brood Care	With Brood Care	Without Brood Care	With Brood Care
Clopea harengus (Herring)	Spinachia vulgaris ( )	Cyprinus carpio (Carp)	Gasterosteus aculeatus (Stickleback)
30,000	150-200	200,000 to 7,000,000	80-120

Some fishes lay still greater numbers of eggs:

Lota vulgaris (Eelpout)	1 million
Hippoglossus vulgaris (Sea Horse) . . .	3 "
Acipenser sturio (Sturgeon)	6 "
Gadus morrhus (Codfish)	9 "

There is likewise a great span in the number of eggs laid by the amphibians. It has been estimated that the maximum number of eggs laid by an amphibian species, for example, the bullfrog, is probably around 35,000. (9). On the other hand, The Urodela, which are more terrestial, may have less than 100. The correlation with brood care is strikingly evident in the following table from Wunder (14).

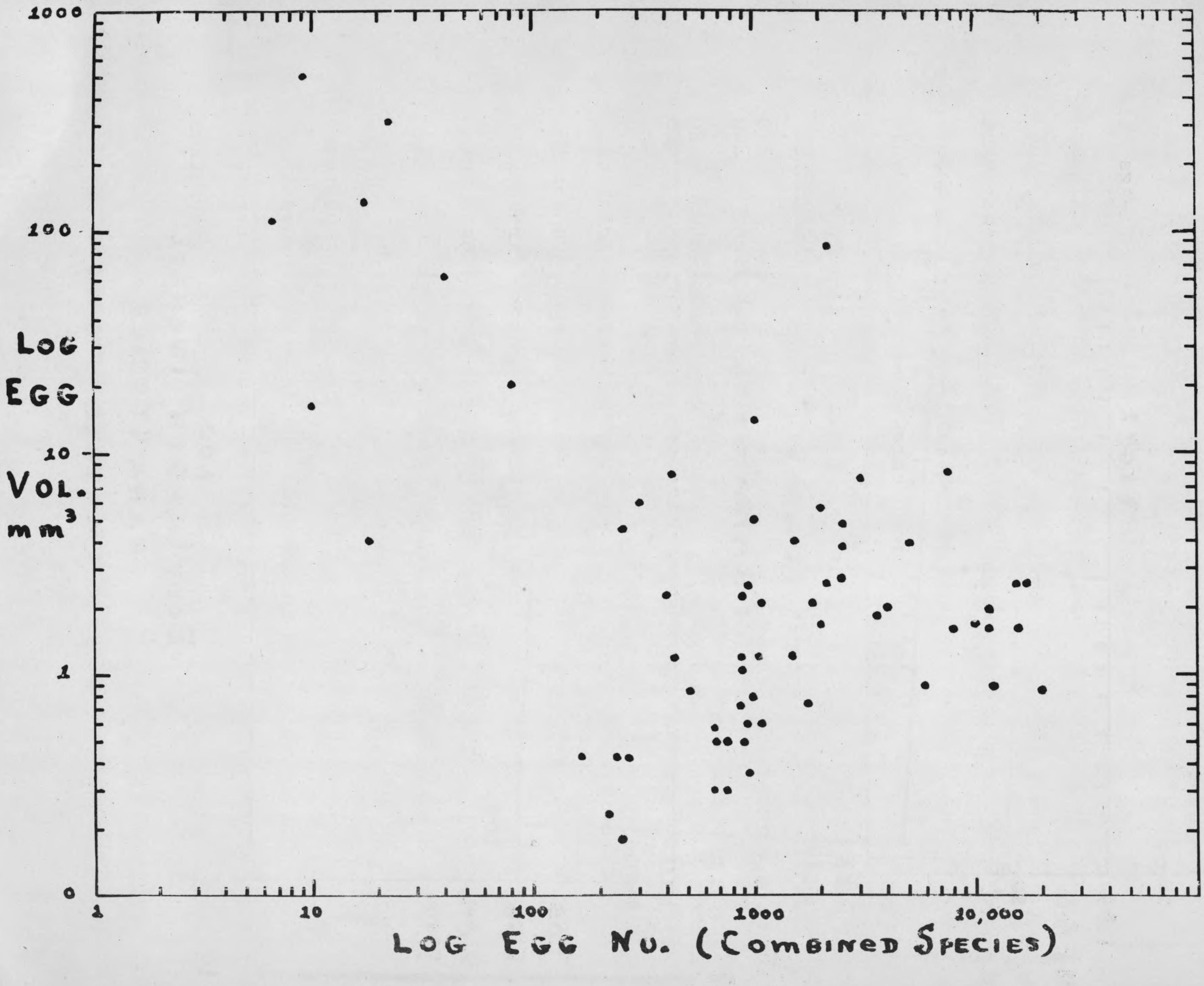
Without Brood Protection		With Brood Protection	
Bufo lentiginum	28,000	Alytes obstetricans	270
Rana esculenta	10,000	Nototreme marsupiatun	200
Bufo viridis	10,000	Pipa americana	60-70
Bufo vulgaris	5,000	Rhacophorus reticulatus	20
Rana temporaria	3,000	Rinoderma darwinii	18
Hyla arborea	1,000	Nototrema pygmaeum	4-7

Even within one genus, there may be a great variation. In the frog Nototrema marsupiatum about 200 eggs are formed; the young are released from the parental body as larvae. In contrast, Nototrema pygnaeum produces only 4 to 7 eggs but these are produced as completely developed frogs.

II. Brood Size and Brood Care in Amphibia

The redundancy devices used and the type of brood care vary considerably from species to species. This makes it very difficult to decide precisely if a relation exists between redundancy of progeny and brood care. For this reason,

Fig. 1



1000
100
10
1
0
Log
Egg
Vol.
mm³
1
10
100
1000
10,000
Log Egg Nu. (Combined Species)

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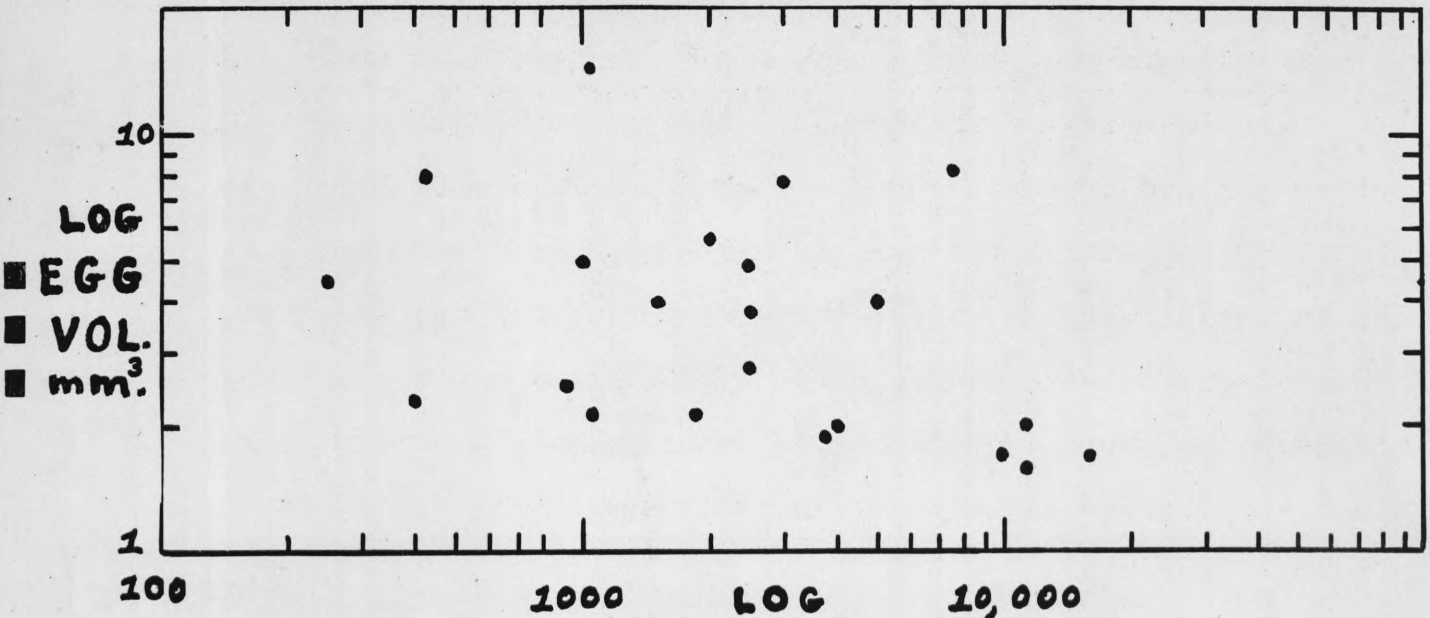
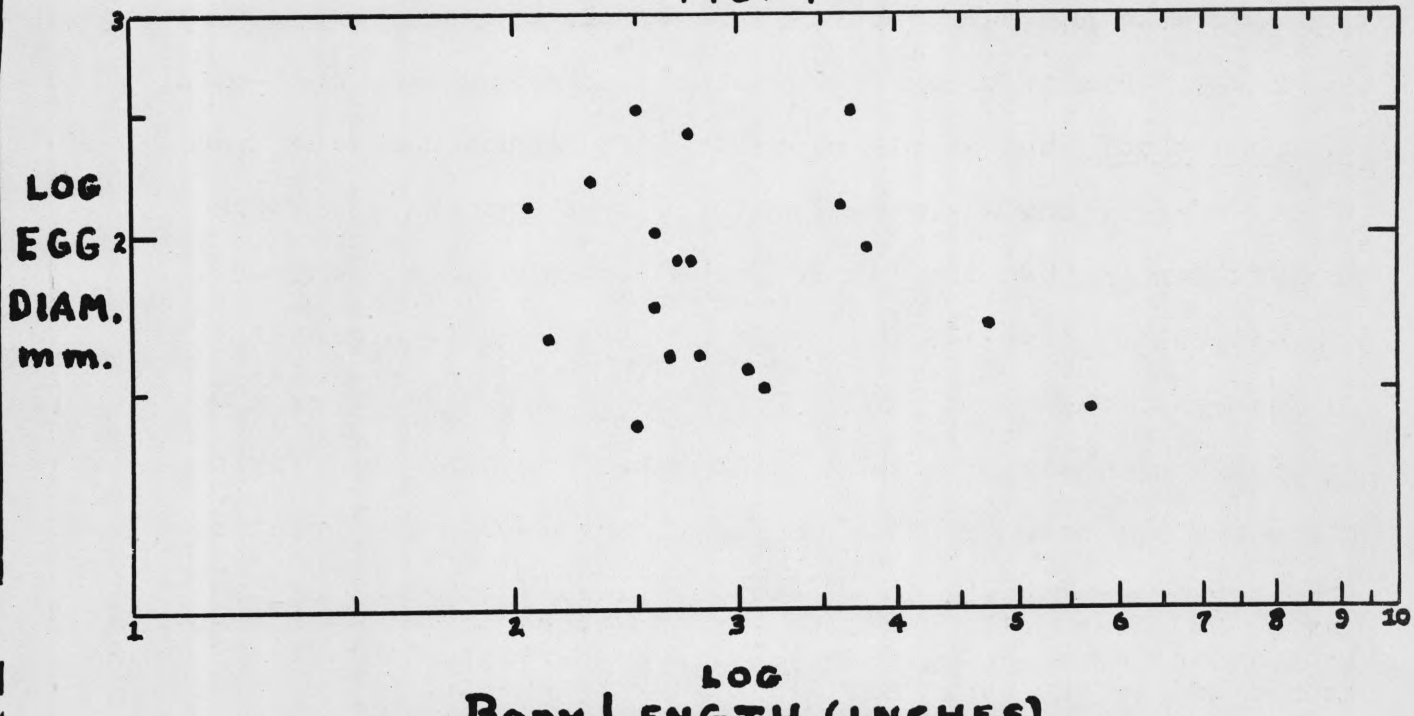
FIG. 2



EGG No.

(RANA SPECIES)

FIG. 4



LOG

BODY LENGTH (INCHES)

RANA SPECIES

(MATURE FEMALES)

attention was confined to the amphibians, since they possess extremes in egg number, variations in egg size, types of embryonic development, compressed larval periods, and brood care.

The majority of the amphibian species employs the oviparous method of development, both with and without brood protection. Commonly, the eggs of most frogs and toads are laid in an aquatic or semi-aquatic environment. Some of them are floated on the water surface but most of them are deposited beneath the surface. The tailed amphibians or salamanders are both aquatic and terrestrial in their egg laying habits.

A. Egg Size

A large egg with a large yolk provides for a certain amount of post-natal brood care; it also represents a certain effort of the parent organism. Therefore, one might expect that egg size and egg number are inversely related. In a very rough way, this is true. For instance, the American bell-toad, Ascaphus truei, has a yolk diameter of 5 mm and deposits from 35 to 50 eggs, while the frog, Mantophryme robusta (7) which is peculiar in that the male carries the eggs in a clump on its underside, lays about 17 eggs of 6 to 7 mm in diameter. In contrast, the common toad, Bufo americanus, lays from 4000 to 35,000 eggs of 1.0 to 1.4 mm in size.[2] However, this relation does not hold in detail. Fig. 1 shows that the relation

[2]The egg of amphibians is characteristically composed of two parts, an outer jelly envelope (or long tube of jelly) and an inner vitellus or yolk. The yolk is incorporated into the embryo and is the basis for all egg measurements.

between egg volume and egg number is not absolute; average values of egg volume (5, 8) are plotted against the average egg number (5, 7, 10, 13, 15) for Anura (the tailless amphibians). The species tabulated represent animals ranging from those which get no brood care to those that receive a great amount of brood care. Fig. 2 shows the same type plot for only the Rana species (frogs).

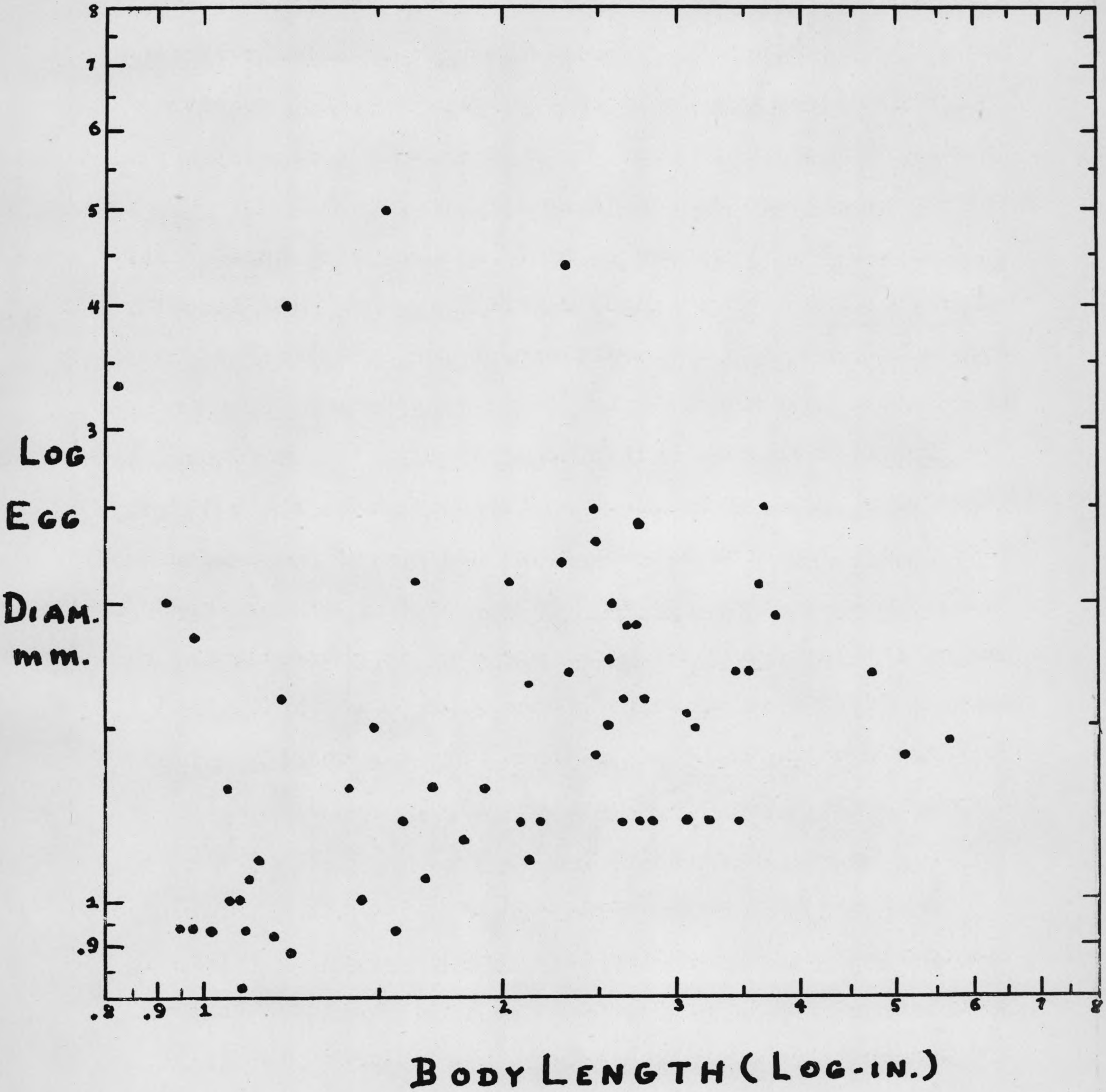
From the data on the combined genera, one can see that there is a very large range, several orders of magnitude, in egg volume and in egg number; except for the extremes, there is no significant correlation between egg size and egg number.

There is another indication that egg size is altogether not a very critical factor. In the Northeast, the bullfrog, Rana catesbiana (our largest frog) has one of the smallest vitelli (yolk) and Rana sylvatica, one of the smaller frogs, has one of the largest (12). That egg size is generally not related to body size is evident from Figs. 3 and 4 (11, 15). Yet, the manufacturing of the same size egg should represent a larger effort for a smaller animal.

B. Larval Compression

A special pre-natal variation of oviparity usually associated with larger egg size is larval compression. This is an extension of the protected development period. Barbour (2) and Wunder (15) describe several foreign species of frogs where the tadpole stage is passed entirely within the egg.

7 I G. 3



COMBINED SPECIES

MATURE FEMALES

In one form, Rana opisthodon, the embryos develop within a hard shell and no tail or gills are formed. The number of eggs laid is relatively small, on the order of 20 to 30. Likewise, an American species with larval compression, Syrrhophus campi, deposits about 6 to 7 eggs (13). As would be expected, the egg size (yolk) is very large (3-4 mm. in diameter).

A few of the amphibians such as the salamander, Salamandra maculosa (15) and the African wood-toad, Nectophyrynoides tornieri (2, 7) are ovoviviparous (live-bearing). The eggs are commonly retained in the oviduct from which the fully developed young emerge. In Salamandra atra, an alpine salamander, 30 to 40 eggs are laid but only one continues to full development in each oviduct (7).

There are no true viviparous amphibians although a few forms approach this condition. Two species of Nototrema are equipped with leaf-like and bell-like gills which may serve as placentas (7). Similarly the embryos of a South American blindworn, Typhlonettes compressicauda have special leaf plates which can be easily used for absorption of food.

C. Post-Natal Brood Care

The amphibians have been classified according to type and amount of brood protection. A type of brood protection, more common to the salamanders than the frogs and toads, is the guarding of eggs and young by the parent, either up until hatching or beyond hatching. Various other means such as transport of the eggs or tadpoles during part or all of their development are observed. The procedure is often modified so that the eggs are retained in brood pouches on the dorsal or ventral surface. In Protopipa aspera and Pipa americana this is so highly evolved that the eggs are placed within separate capped cavities on the back where they develop into tadpoles. Other species allow for the full term of development either in the mouth or in the vocal sacs of the male. The characteristics of the live-bearing species have already been mentioned.

Wunder (15) has reviewed the amphibia and classified them according to the kinds and amount of brood care. A modification of this classification is presented in an intuitive order of importance in Fig. 5, and related to the (log of the) egg number. The data refer mostly to Anura and to a few Urodeles. The relation between brood size and brood care is immediately noticeable.

Discussion

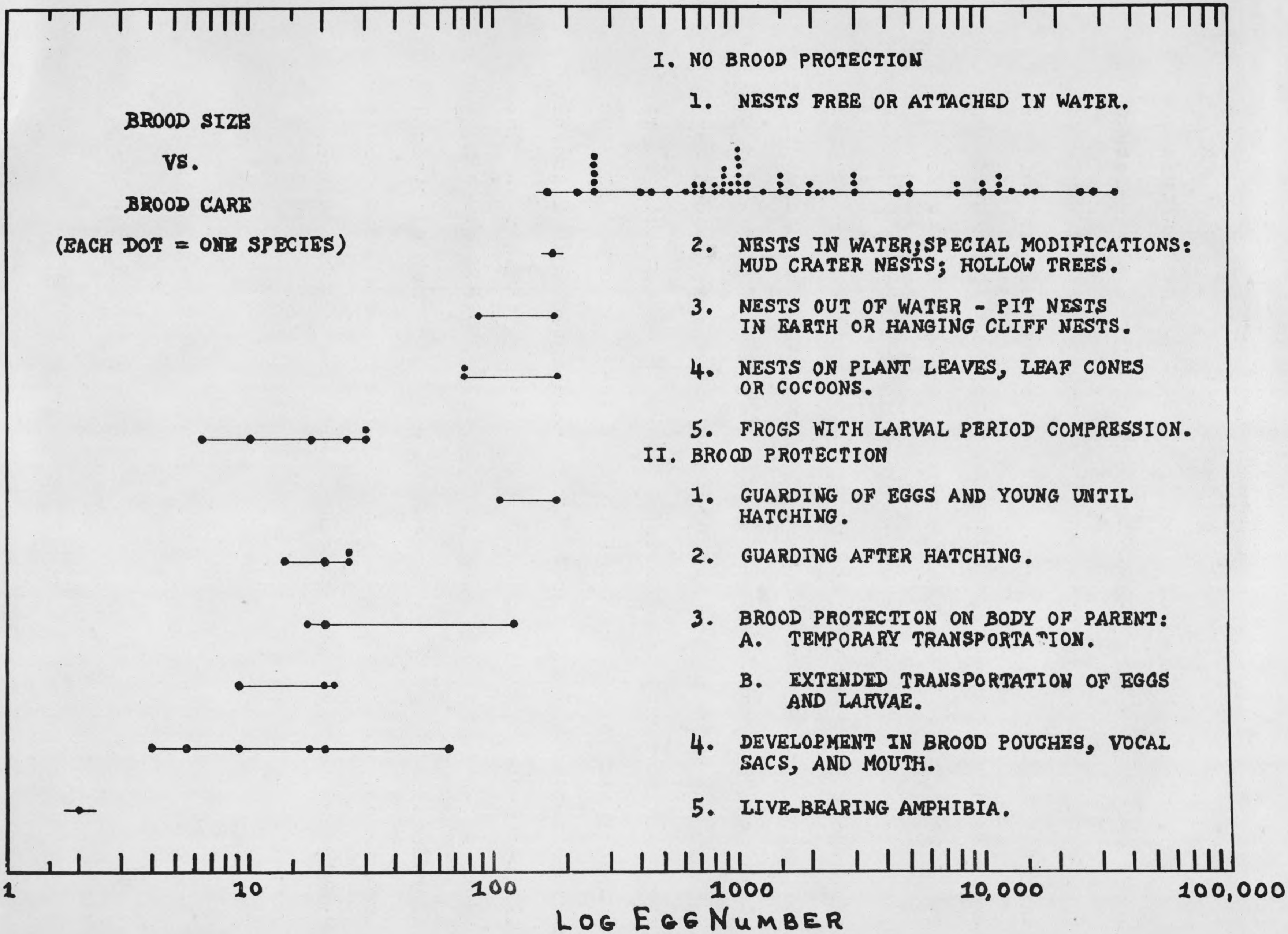
Scattered observations on the relationship between egg size and egg number in the past have led some to conclude that these factors are inversely related. The results here indicate that only in the extreme cases is this true and in general there is no significant correlation between an increase in egg size and a decrease in egg number.

Similarly, it was found that the egg size (volume) is not simply regulated according to the size of the adult producing it, except in isolated instances.

However, a review of biological literature confirms our guess that brood size and brood care are inversely related. It also shows that between closely related species there are vast differences in the amount of redundancy used. This is in striking contrast to a conclusion reached from reviewing a related field (10B). In identical twinning it was found that there is a certain amount of redundancy built into each egg, which manifests itself in the potentialities of identical twinning; this amount varies very little throughout the whole animal kingdom.

It may be assumed that, for any given species and any given environment, there exists a certain combination of redundancy and care which represents a least effort. If such a combination exists, and if it is associated with a sharply limited amount of redundancy, then one might expect that natural selection will have fixed this value. The great range of redundancy used in reproduction suggests that a critical amount does not exist, but that redundancy and brood care are freely and widely interchangeable yielding results which vary little.

FIG. 5.


BROOD SIZE
VS.
BROOD CARE
(EACH DOT = ONE SPECIES)
I. NO BROOD PROTECTION
1. NESTS FREE OR ATTACHED IN WATER.
2. NESTS IN WATER; SPECIAL MODIFICATIONS: MUD CRATER NESTS; HOLLOW TREES.
3. NESTS OUT OF WATER - PIT NESTS IN EARTH OR HANGING CLIFF NESTS.
4. NESTS ON PLANT LEAVES, LEAF CONES OR COCOONS.
5. FROGS WITH LARVAL PERIOD COMPRESSION.
II. BROOD PROTECTION
1. GUARDING OF EGGS AND YOUNG UNTIL HATCHING.
2. GUARDING AFTER HATCHING.
3. BROOD PROTECTION ON BODY OF PARENT:
A. TEMPORARY TRANSPORTATION.
B. EXTENDED TRANSPORTATION OF EGGS AND LARVAE.
4. DEVELOPMENT IN BROOD POUCHES, VOCAL SACS, AND MOUTH.
5. LIVE-BEARING AMPHIBIA.
1
10
100
1000
10,000
100,000
LOG EGG NUMBER

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